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BULLETIN

OF THE

TORREY BOTANICAL CLUB

FEBRUARY, 1918

On the constancy of cell shape in leaves of varying shape

LILLIAN A. TENOPYR

(WITH ONE TEXT FIGURE)

INTRODUCTION

Since the publication of Sanio's observations on the size of the wood cells of *Pinus sylvestris*, the subject has aroused considerable interest, as is shown by the work of Amelung, Sachs, Strasburger, Gates, Keeble, Neilson Jones, Jakushkine and Wawilow, and Sierp. Among the zoologists who have investigated the same problem are Gaule, Donaldson, Hardesty, Levi, Morgan, Driesch, Rabl, Chambers, Popof, Berezewski, Jennings, and Conklin.

Sanio (1872) shows that in the Scotch pine, the wood cells attain a definite (final) size, which is constant for the following annual rings. He finds, however, that the size of the wood cells does vary according to the height at which they are situated in the stem. The size of the wood cells increases as the stem is ascended, until a maximum is reached, then decreases toward the apex. The branches always have smaller wood cells than the main stem at the level at which the branch arose; but branches which arise from that portion of the main stem which had the largest wood cells, have also larger wood cells than the branches situated higher or lower on the stem.

Amelung (1893) studied cell size in its relation to the size of the organ. He raised the question whether differences in the size of homologous organs within a species are accompanied by corres-

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ponding variations in cell size, or whether the cell size of each species is a constant and distinct character. That is, do environmental conditions, which modify the size of plant organs, affect the size of their cells? Are giants and dwarfs due to greater or lesser development in size of the individual cells, or to more or less numerous cell divisions?

Amelung estimated the size of the various cells of plants having homologous organs differing in size. He made ten longitudinal sections, or, in other plants, ten cross sections of each of the organs to be compared. These he mounted in water or in glycerine. In each section he counted the number of cells of a given tissue that were intersected by a line on the stage micrometer, a line usually 1 mm., sometimes 5 mm., in length. He thus obtained ten cell counts on each organ. From these he determined the average number of cells to 1 mm. and the average length or average breadth of the cells of a given tissue both of the giant and of the dwarf organs. He compared the palisade and epidermal cells of large leaves with similar tissue cells of small leaves, the wood cells of poorly developed and of well-developed shoots, and the parenchyma of large and small fruits. The organs compared were taken from the same plant, or from different plants of the same species, or from closely related species. He found that the cell size of a given tissue of an organ is constant for the species, regardless of the average size of the individual or of the organ. Thus, the epidermal cells of a small leaf of *Ficus macrocarpus* were as large as those of a leaf twice as long and broad; the wood cells of a twig of *Vitis vinifera*, 6 mm. in thickness, measured as much in cross section as those of another shoot, only half as thick; a leaf of *Victoria regia*, measuring 900 × 900 mm., and one of *Nymphea alba*, 190 × 190 mm., had cells that were identical in size.

Amelung concludes that not the cell size, but the cell number, determines the size of an organ.

Sachs, with whom Amelung worked, confirms the statement that the cell size of a given species is constant, and is not influenced by body size.

Strasburger (1893), in a series of studies on the relation of nuclear and cell size in the embryonic cells of the growing points

of stems and roots of many species of plants, reached the same conclusion, regarding the size of these cells in large and small individuals of the same species, although varieties of the same species may differ greatly as to their cell size.

Conklin (1912) has made an elaborate and extended study of cell size compared with body size in the genus *Crepidula*. He found great variability in the body size of these gasteropods. In *Crepidula plana*, there are dwarf and normal females. These latter are larger than the normal-sized males. The average size of individuals of the same sex differs greatly for the different species. Yet, in spite of all these differences in body size, the tissue cells of corresponding organs or parts of organs were in general of the same size in all the adult animals examined.

The muscle fibres and ganglion cells formed an exception to this rule. In *Crepidula plana*, the size of these cells was greater in the largest animals. This, he notes, agrees with the observations of Gaule, Donaldson, Hardesty, and Levi, who measured these cells in frogs and various mammals. In connection with the size differences found in these cells, Conklin cites the observation made by Levi, that these cells cease to divide early in life, whereas such cells as the epithelial and the gland cells, where Levi found no correlation with body size, continue to divide throughout life.

The size of the sex cells, also, varied in the different species. In general, the smaller species produced larger eggs. These resulted in larger embryos, having larger cells. Conklin says the fact that the species with smaller eggs produce, in the end, larger adults, and that the final cell size is almost the same for all the crepidulas, is due to a longer duration and more rapid rate of cell growth and division in the larger species.

A very notable case bearing on the question of the constancy of cell size in a species, is that of *Oenothera gigas*, a so-called mutant of *Oenothera Lamarckiana*, with double the number of chromosomes found in the parent species. Gates (1909) found that the cells of *Oenothera gigas*, which have twenty-eight or twenty-nine chromosomes, were conspicuously larger than the cells of *Oenothera Lamarckiana*, whose chromosome number is only fourteen.

Boveri (1905), on the basis of extended studies on sea-urchin larvae, formulated the law that the cell size in sea-urchin larvae

is directly proportional to the number of chromosomes. According to this law, one would expect to find here a direct relation between the amount of chromatin, the nuclear size, and the size of the cell. Gates (1909) does not find that this holds equally for all the tissues. While the chromosome number of *Oenothera gigas* is double that of *Oenothera Lamarckiana*, the cells of the former are not uniformly twice as large as those of corresponding tissues of *Oenothera Lamarckiana*.

Gates estimated the size of rectangular cells, as those of the epidermis, by multiplying the three dimensions. The length and breadth of the cells he estimated from measurements made on camera-lucida drawings, magnified about 1,380 diameters, the third dimension being considered as identical with the length of the cell. By length of the cell he means the measurement along the long axis of the organ, though this is not necessarily the longest dimension of the cell; the width being the measurement at right angles to the surface of the organ, that is in the direction of the thickness of the organ in which it occurs. The epidermal cells of the petals of *O. gigas* were 1.9 times as large in volume as those of *O. Lamarckiana*, which is closely in accordance with Boveri's law. However, other tissue cells depart widely from the expected ratio of 2 : 1. The stigmatic cells, the cells of the anther epidermis, and the inner wall of the anther, were more than three times as large in *O. gigas* as in *O. Lamarckiana*, while the pollen mother cells of the former, both during synapsis and in the reduction divisions, were only 1.5 times as large.

Moreover, the increase in size of the *O. gigas* cells was not equally great in all dimensions. The epidermal cells of the anther increased 72.8 per cent. in length, and only 28.4 per cent. in width; the stigma cells increased 51.9 per cent. in length, and 32.2 per cent. in width. The anthers of *O. gigas* are approximately twice as long as those of *O. Lamarckiana*. Gates believes that both have approximately the same number of cells, "and that the greater length of the *O. gigas* anthers is accounted for by the greater length of the individual cells." Gates concludes that there is evidently some regulating factor determining that the increase in length of the epidermal cells shall be greater than the increase in their width, in the anther epidermis, but less in the petal epidermis.

Similarly, Keeble (1912), in a comparative study of the cells of the stem and leaf tissues of White Queen Star, a horticultural variety of *Primula sinensis*, and those of its mutant, Giant White Queen Star, showed that the latter is a giant because its cells are larger and not because they are more numerous than those of the parental type. Indeed, in the cortex of Giant White Queen Star, Keeble found fewer cell layers than in the normal type. The measurements he gives for the cortical cells of the flower peduncles, taken for the layer immediately external to the endodermis, are:

Radial measurements . . . . . $g : n :: 100 : 48$
Tangential measurements . . . . . $g : n :: 100 : 81$
Longitudinal measurements . . . . . $g : n :: 100 : 57$

The cells are larger in all three dimensions, radial, tangential and longitudinal, and the gigantism is common to all tissues. He does not state how many cells were measured nor does he describe his methods. The chromosome number in both varieties is the same. The nuclei of the giant form are larger, as Keeble shows in his drawings of pollen grains, but he does not give any measurements of them. It is therefore impossible to tell, in the case of White Queen Star and its giant mutant, Giant White Queen Star, whether or not the amount of chromatin material is the factor determining the relative cell size in these plants.

In *Avena sativa*, Jakushkine and Wawilow (1913) found that different varieties may have different-sized cells, but they were unable to discover any relation between the size of either the stomata or the epidermal cells, and that of the leaf surface, when varieties with different-sized organs were compared. For instance, a small-celled variety had the largest leaves. Like Sanio these authors found that the cell size of the leaves varied according to their position on the stem, the cells of the highest leaf being smaller than those of the third leaf from the top of the stem. They found that in any given variety, the cell size of any tissue at a definite part of an organ was a constant character, and further that each of the seventeen pure lines obtained through selection from a mixed population of German and west Russian oats, fell into one of two groups, namely:

1. A large-celled group, the average length of the stomata of the highest leaf being 0.063 mm., that of the third leaf down being 0.0735 mm.

2. A small-celled group, the first leaf from the summit having stomata whose average length is 0.054 mm., those of the third leaf being 0.067 mm. long.

In his paper on species hybrids of *Digitalis*, Neilson Jones (1912) does not give any measurements of the cell size of *D. grandiflora* and *D. purpurea;* but his general observations are most interesting. He finds that *D. grandiflora*, which has smaller leaves than *D. purpurea*, has larger leaf cells. Hybrids of these two species are intermediate in both external and cytological characters, but in both respects there is a tendency to favor the seed parent. Thus, in the hybrid resulting from the cross *p.* ♀ × *g.* ♂ the leaves are somewhat larger and the cells smaller, than they are in the progeny of the reciprocal cross. Evidently the size of the leaves and cells of the hybrids cannot be due to heterozygosity, since in that case we would expect the reciprocal crosses to have the same effect on the leaf and cell size of the resulting hybrids.

One of the most careful studies of the relation between body size and cell size is that of Sierp (1913). He made measurements of the cells of various tissues of dwarf and normal plants, the dwarfness being in some cases a fluctuating characteristic, in other cases hereditary. Under the first group come dwarfs of *Panicum sanguineum*, *Draba verna*, *Aethusa Cynapium* and *Urtica dioica*. This type of dwarfs always had cells more or less reduced in size. Some of the differences in cell size were very slight. True, that is, hereditary dwarfs, he found were of three kinds:

1. Those having smaller cells than the normal plants, as certain dwarf varieties of *Solanum tuberosum*, *Pisum sativum*, *Clarkia pulchella*, and *Zea Mays*.

2. Dwarfs with cells slightly smaller than, or almost the same as, those of the normal type, as those of *Lathyrus odoratus*, *Mirabilis Jalapa*, *Phaseolus vulgaris*, and *Lens esculenta* (Rote Kleine Winter).

3. Dwarfs with larger cells than found in the normal plants, as *Nigella damascena nana*.

Sierp found great variability in the cell size of each tissue, though the average value was quite constant. He lays great stress on the importance of measuring exactly corresponding places, when comparing cell size of any tissue of the stem or leaf,

since it varies according to the height of the stem. Moreover, in each leaf, the cells at the apex, at the base, and midway between these two regions differ in size.

Sierp used the Schwendener-Ambronn method for finding the average cell size. This method gives the average area of the cell from a surface view, or of its cut surface in longitudinal or cross section. A camera-lucida drawing is made of a group of the cells of the epidermis, or of the cells of any other tissue, of each of the organs compared. These drawings are made on a piece of Bristol board of as uniform thickness as possible, the area and weight of this piece of Bristol board being carefully noted. The drawing of the group of cells is then cut out and weighed also. The product of the weight, times the area of the original piece of Bristol board, divided by the weight of the camera-lucida drawing, gives the area of the group of cells drawn. This area, divided by the number of cells in the group, gives the average area of the cell. The area of the organs compared is ascertained in a similar way.

Possibility of error lies in the uneven thickness of the Bristol board, in its absorption of moisture from the atmosphere, and in the lack of precision in cutting inside or outside of, not through, the outline of the group of cells. However, as many tissue cells, especially those of the epidermis, are very irregular, this method of determining cell size would seem preferable to that of basing one's comparisons on the average length or average width of the cell or on the product of these two dimensions, as if the cells were indeed rectangular.

The work of Sanio, Amelung, Jakushkine and Wawilow, and Conklin seems to warrant the conclusion that while the cells of an organ may differ greatly in size for various and obscure reasons, the average cell size of an organ is constant for the species or variety. The work of Gates, Keeble, Neilson Jones and Sierp shows that hereditary differences in body size of varieties or species may be due to corresponding or reverse differences in cell size, in cell number, or to both these factors.

THE PROBLEM OF CELL FORM

The further questions suggest themselves: Is there any correlation between the shape of the plant organ and the shape of its con-

stituent cells? Are the long narrow stem leaves of many plants due to the length and narrowness of their cells as compared with those found in the more rounded basal leaves, or to a greater number of cell divisions in the long axis of the leaf? Are the cells of the lobes of incised leaves wider than those of the constricted portions of the leaves, or are the constrictions the result of a slower rate or shorter duration of cell division?

Gates (1909) seems to think such a direct relation between cell shape and leaf shape is probable. "Increase [in cell size]," he says, "has been greater in one dimension than in another, resulting in a change in the relative dimensions of the cells. This in all probability accounts for the altered shape of some of the organs, as leaves and capsules." He holds that the greater cell size, together with the difference in cell shape of *O. gigas*, is sufficient to have produced external differences between the two plants, without the introduction of any new factors. Except for stating that the anthers of *O. gigas*, which are about twice as long as those of *O. Lamarckiana*, have cells which are not only larger but relatively longer than those of the parent plant, Gates does not give any comparative measurements on corresponding dimensions of organs and their cells, to prove the relation of cell shape and body shape.

According to both Familler (1900) and Goebel (1908) there is a direct relation between the light intensity and the form of leaf produced in *Campanula rotundifolia*. Plants placed where they were well shaded, instead of developing typical linear stem leaves, produced only round leaves on the stem, similar to the basal leaves which appear earlier in spring.

In my cultures of *Lobelia Erinus*, plants grown in the greenhouse during the dull winter months flowered less profusely than during the summer. These winter plants had only spatulate leaves along the whole length of the floral shoot and none of the small linear leaves which are usually found on the upper part of the stem.

Familler's explanation for such phenomena is that the light, food supply, and other optima are higher for the production of the flowers and the long leaves than for the production of the round leaves. Thus, it is not until the warm weather of early summer,

when the illumination is stronger and the plant already possesses a well developed root system and numerous basal leaves, that the narrow stem leaves and flowers appear. Even then, a diminution of the light intensity, or any great disturbance in the development of the plant can occasion the production of the juvenile form of leaf. Thus, if the *Campanula* plant is propagated by cuttings from shoots bearing only long narrow leaves, the young leaves sent out by these plants are round, like the basal leaves of the parent plant. These propagated plants cannot produce long leaves until they have better developed root systems, and the plants have become well established in their new food relations.

I have studied the shape, i. e., the relation of length to breadth of leaves and their constituent cells, in the following three types of plants.

1. Species with broad basal leaves, narrow stem leaves near the inflorescence, and transitional leaves on the lower part of the stem: *Campanula rotundifolia, Lobelia Erinus.*

2. Broad-leaved and narrow-leaved species belonging to the same genus: *Plantago major* and *P. lanceolata, Linum angustifolium* and *L. usitatissimum.*

3. Varieties of the same species having entire leaves, as compared with others having lobed leaves: *Cichorium Intybus.*

METHODS

The Schwendener-Ambronn method used by Sierp, which gives the average area of the cells, was not suited for my investigations on the relation of the length to the breadth of the cells of variously shaped leaves. The method used in finding the average length and the average breadth of the cell resembles that of Amelung, except that an ocular micrometer instead of a stage micrometer was used. The number of cells to a unit of the scale in the ocular micrometer were counted, and the average dimensions in millimeters were estimated from these numbers. Whenever the line of measurement passed through the two opposite sides of a cell, as it appeared in the section regardless of how small a fragment of the entire cell was thus cut, its measurement was recorded as the measurement of the length or of the breadth of the cell in that particular portion of the leaf. If, as sometimes happened in the irregular cells of the epidermis, the same line passed twice through

any cell, the two fragments were recorded together as the measurement of the cell in that region. Frequently the end of the line of measurement did not reach the opposite wall of a cell. In such a case I estimated as accurately as possible what fractional part of the length or of the breadth of that cell fell upon the line of measurement, and this fraction was recorded. Thus, if the line passed through nine cells and reached only one fifth of the way across the tenth cell, the cell count was recorded as nine and one fifth cells. This method cannot of course be regarded as giving absolute length and breadth of the epidermal cells especially, but is probably the best available. It seems on the whole preferable to record the fractional parts of cells lying on the scale unit. The alternative would be to make all the measurements on single cells, and in this method the problem of selection and the errors in determining the cell axes would probably involve still greater inaccuracies.

The maximum length and width of each leaf examined was recorded, and an outline tracing was made. In most cases one hundred counts were made on each type of leaf as the basis for comparison, with the exception of *Linum*, in which case I made nineteen counts on the palisade cells and forty-five counts on the epidermis, and of the palisade cells of *Plantago*, on which thirty counts were made.

Except in the comparison of leaf shapes in lobes and constrictions, the cell counts were made in the middle region of the leaf, and about 2 mm. away from the midrib. As the comparison was between leaves differing from each other in length and breadth, only these two dimensions of their cells were measured. I have not concerned myself with the third dimension, as the difference in thickness of the leaves is too small for easy study.

All the measurements were made from the surface of the leaf. The epidermal cells of the under surface of the leaf were measured from below. The palisade cells were measured from above. Thus in any one portion of a given tissue I could make measurements of the length and of the width of the cells at the same time. The length of the cell I considered to be that dimension of the cell which was parallel to the midrib of the leaf and the long axis of the entire leaf, the width of the cell as taken was the dimension corresponding to the width of the leaf.

I found that, if the sections of the lower epidermis to be measured were prepared by stripping this tissue away from the leaf, it was difficult to determine which axis of the cell had been parallel to the midrib. The possibility of error in this respect was greatest in cells having irregular outlines. I therefore prepared these sections by removing the upper epidermis and the green tissues from that portion of the leaf which was to be examined, leaving the lower epidermis intact. The entire leaf, or the exposed epidermis with a portion of the midrib, was then mounted in water and placed under the microscope. Before measuring the palisade cells, both the upper and the lower epidermis of the region to be examined were stripped off, care being taken to remove none of the green tissue. When the leaf was placed flat on a slide the remaining tissues were sufficiently transparent to enable me to make measurements of the two dimensions of the upper ends of the palisade cells. All the measurements were made on the living cells, thus avoiding the possibility of shrinkage or distortion due to fixation.

I found an ocular micrometer preferable to a stage micrometer, as, by moving the slide or by rotating the micrometer, I could more easily bring the specimen to be examined in the proper position in relation to the scale, without handling the specimen itself.

Throughout the investigations I used a Leitz ocular micrometer. The scale consists of a large square, divided into four smaller squares, one of which is again divided into twenty-five equal squares. The value of these divisions of course depends upon the magnification, and it was ascertained with the aid of a stage micrometer for each eye-piece and objective used. For example, when a one-inch ocular and two-thirds objective were used with a Bausch and Lomb microscope, each side of any one of the smallest squares was equal to 0.116 millimeter. All cell counts on all the plants examined are stated in terms of cell diameters per millimeter.

The section to be measured was placed on the stage of the microscope in such a position that the midrib of the leaf was parallel to one side of the ocular micrometer scale.

In measuring the palisade cells, a favorable area of this tissue, uncrushed and free from veins, was chosen, equal to one of the

smallest squares of the ocular micrometer. The number of cells cut by each side of the square was counted. The length of this line was then divided by the cell number to obtain the average cell diameter. In this way, with one placing of the micrometer, I could make four measurements, two giving the length and two giving the width of the palisade cells of the region.

To measure the epidermal cells, a suitable area, free from veins, was selected. To avoid errors due to the presence of stomata, care was taken in each case to so place the micrometer that the stomata came between but not on the lines of measurement. In plants having numerous stomata, this was often a difficult matter. In this case I used twice as large a micrometer unit, the sides of two squares, corresponding roughly to the larger size of the cells.

CAMPANULA ROTUNDIFOLIA

Campanula rotundifolia is well known as a plant whose radical and cauline leaves differ widely in shape. It produces numerous radical leaves, which are often wanting at the time of flowering. These are petioled, almost orbicular in shape, with cordate base. In May or June the plant sends up several shoots which bear flowers at their summits throughout the summer. The upper stem leaves are sessile and linear, but the lower stem leaves are intermediate in shape, being ovate and acute. These three types of leaves are designated in the tables as basal, transitional, and linear.

Measurements were made of the length and the width of the cells of the lower epidermis of typical leaves of the three forms described. TABLE I gives the results of these measurements. The average number of cells in each leaf that were cut by a line 1 mm. in length, is given for each of six leaves of each shape. The final averages are from the original data and differ fractionally from the average of the averages in the following table.

A comparison of the average number of cells to 1 mm. found in the long and the broad axis of each basal leaf shows that there is some variation in the size of the cells, for example, in leaf *C* the average number being 22.02 cells to 1 mm. in the long axis and 20.91 cells in the transverse axis, while in leaf *D* the cell counts were 26.95 cells in the long axis and 29.56 cells in the transverse axis of the leaf. These figures also serve as an example of the variability

found in the relative dimensions of the cells, the cells in leaf *C* being somewhat broader than long, while in leaf *D* this relation of length to breadth of the cells is reversed. This variability in cell

TABLE I

CAMPANULA ROTUNDIFOLIA

Comparative length and width of the three types of leaves and the corresponding dimensions of the cells of the lower epidermis of each type of leaf. Numerals in parentheses show number of counts. Line of measurement = 1 mm.

	Basal leaves		Transitional leaves		Linear leaves	
	Length	Width	Length	Width	Length	Width
Leaf *A*	11.	14.5	23.	5.5	56.	3.
Average cell size (15)	0.037	0.036	0.04	0.029	0.033	0.03
Average number of cells (15)	26.99	27.74	24.81	33.45	29.78	32.97
Leaf *B*	15.	17.	49.	8.5	32.	3.
Average cell size (15)	0.046	0.047	0.038	0.038	0.036	0.035
Average number of cells (15)	21.54	21.38	26.02	25.92	27.75	28.
Leaf *C*	17.	18.	55.	8.	39.	4.5
Average cell size (15)	0.045	0.047	0.035	0.036	0.033	0.034
Average number of cells (15)	22.02	20.91	28.52	27.55	29.98	28.92
Leaf *D*	13.	11.	20.	8.	49.	3.
Average cell size (15)	0.037	0.033	0.043	0.037	0.03	0.027
Average number of cells (15)	26.95	29.56	25.95	26.56	32.28	35.77
Leaf *E*	10.	12.5	27.	6.	50.	3.
Average cell size (15)	0.042	0.037	0.035	0.036	0.032	0.033
Average number of cells (15)	23.55	26.97	28.3	27.32	30.6	29.86
Leaf *F*	19.	19.	21.	6.	57.	3.5
Average cell size (25)	0.037	0.039	0.037	0.03	0.04	0.032
Average number of cells (25)	26.74	25.62	26.61	32.36	24.7	30.31
Average measurement of leaves	14.16	15.33	32.5	7.	47.16	3.33
Average measurement of cells (100)	0.04	0.039	0.038	0.034	0.034	0.032
Average number of cells (100)	24.85	25.34	26.26	29.21	28.74	30.91
Ratio dimensions of leaf	.92 : 1		4.64 : 1		14.15 : 1	
Ratio dimensions of cell	1.02 : 1		1.11 : 1		1.07 : 1	

size and cell shape is found in all three forms of leaves examined. However, in most leaves as in the final averages, the numbers indicate that the cells are nearly isodiametric or somewhat longer than they are broad. The table also gives the average measurements of the cells in fractional parts of a millimeter.

A glance at the ratio of the length to the width of the cells of the lower epidermis of the three forms of leaves shows that the percentage of difference between these two dimensions does not approach that found between the leaf dimensions. The basal leaves are on the average slightly shorter than broad, and their epidermal cells are slightly longer than broad, almost isodiametric.

The transitional leaf is more than four times as long as broad, yet its cells are of almost the same shape as those of the basal leaf, being slightly longer than wide. In the linear leaves, which are about 14.15 times as long as they are broad, the cells are only .07 longer than wide. That is, the difference between the length and the width is 287 times greater in the leaf than in the cell. Moreover this difference in cell dimensions is least in the basal leaves and greatest in the transitional leaves. There seems to be no relation here between the shape of the cell and that of the leaf.

The slight difference between the ratios of length to breadth of cells obtained in the different leaves is almost equaled by the variability of the individual cells in any one leaf. In some leaves the cell proportions, as compared with the leaf proportions, may be found reversed in certain areas. Thus fifteen measurements of cells in a basal leaf *E*, which was 10 mm. long by 12.5 mm. broad, showed that the cells averaged 0.042 mm. long and 0.037 mm. wide (a ratio of 1.13 : 1) while similar measurements of cells of a linear leaf, 50 mm. by 3 mm., showed that they had an average length of 0.032 mm. and an average width of 0.033 mm. (a ratio of .97 : 1). The forms of the three types of leaves found in *Campanula rotundifolia* are not therefore directly correlated with the shape of their cells.

The cells of the stem leaves show a smaller average size than those of the basal leaves, the cells of the linear leaves being most reduced. In TABLE II are given the relative length and relative

TABLE II

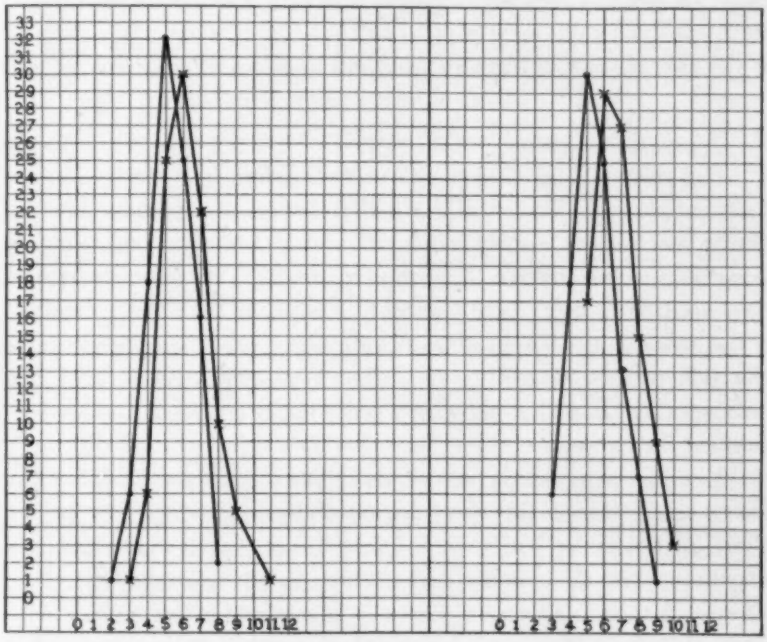
CAMPANULA ROTUNDIFOLIA

Relative size of the lower epidermal cells of the three types of leaves.

	Length of cells	Width of cells
Transitional leaf : basal leaf	.94 : 1	.86 : 1
Linear leaf : basal leaf	.86 : 1	.82 : 1

width of the cells of the three types of leaves. The difference in the dimensions of the three types of cells is very slight, and might seem at first to fall within the limits of individual cell variability. I therefore plotted frequency curves (FIG. 1) showing the number of times that I found a given number of cells to a line of 0.232 mm., in the long and in the broad axis of the basal and the linear leaves. A greater number of cells to a given line indicates smaller cell size.

All cases where there were four and a fractional part of a cell to 0.232 mm. were recorded as four cells—all cases of more than five cells and less than six cells were recorded as five cells, etc. These curves show that both in the long axis and in the transverse



A *B*

FIG. 1. Curves denoting frequency of dimensions of lower epidermal cells of *Campanula rotundifolia*. *A*, Transverse axis. *B*, Longitudinal axis. Abscissas denote the number of cells to 0.232 millimeter. Ordinates record the number of instances in which a given number of cells per 0.232 mm. occurred. Unbroken lines used for cells of basal leaf; lines broken by x's, for linear stem leaf.

axis of the leaf, there are most frequently five cells to 0.232 mm. in the basal leaf, while in the linear leaf there are six. The curves prove conclusively that the decrease in both dimensions of the lower epidermal cells of the linear leaves is regularly present in the material studied.

This observation agrees with that made by Sierp, who found that in *Mirabilis Jalapa*, *Nigella damascena*, and *Pisum sativum* (Laxton's Alpha) the higher the leaf was situated on the stem, the smaller its cell size, as well as that of the node from which the leaf sprang.

Neither in the case of *Campanula* nor the other plants studied did I find the size of the individual cells to be as constant as Amelung's measurements would indicate. Because of the wide range of variation in cell size, the average cell size could be determined only through numerous counts. Usually one hundred counts were made on each form of leaf, so that the average cell size given is the average size of from six hundred to seven hundred cells.

LOBELIA ERINUS

This plant, like *Campanula rotundifolia*, has three distinct forms of leaves. The orbicular radical leaves are developed before the flower shoots appear, and are rarely found at the time of flowering. The slender, somewhat recumbent shoots bear at first only spatulate or obovate leaves, but later, as the stem elongates, it has small linear leaves near its summit. The flowers grow from the axils of these linear leaves. Each type of leaf produced is not only smaller than the one which preceded it but it is also proportionately narrower.

A comparative study was made of the shape of the cells of the lower epidermis of the three forms of leaves, in relation to the shape of the whole leaf. Only those linear leaves were examined in whose axils the flowers had already faded, as I thought these leaves were probably fully grown. Measurements were made on six such leaves after two intervals of two weeks each, to see if they had ceased to grow by the time the flowers had bloomed. There was some further growth, but scarcely enough to seriously affect the proportions of the leaf, or noticeably alter its shape (TABLE III).

TABLE III

LOBELIA ERINUS

Record of further growth of linear leaves, after flowers in their axils had faded. Line of measurement = 1 mm.

Plant	*A*	*B*	*C*	*D*	*E*	*F*
	Length × width	Length × width	Length × width	Length × width	Length × width	Length × width
First measurements...	10 × 1.5	10 × 1	12 × 2	14 × 2	19 × 8	19 × 4
End second week.....	10 × 1.87	11 × 1.5	12 × 2.5	15 × 2.5	—	20 × 4
End fourth week.....	11.5 × 1.87	11 × 1.5	Died	16 × 2.5	21 × 9	20.5 × 4

The results of the cell measurements made are given in TABLE IV, which shows both the number of cells per millimeter and the dimensions of the cell. The ratio of the length to the width of these

TABLE IV

LOBELIA ERINUS

Comparative length and width of the three types of leaves and the corresponding dimensions of the lower epidermal cells of each type of leaf. Numerals in parentheses show the number of counts. Line of measurement = 1 mm.

	Basal leaves		Transitional leaves		Linear leaves	
	Length	Width	Length	Width	Length	Width
Leaf *A*	29.	27.	19.	9.	10.5	2.5
Average cell size (15)	0.066	0.053	0.044	0.048	0.032	0.033
Average number of cells (15)	14.99	18.73	22.8	20.79	30.9	30.11
Leaf *B*	27.	25.	21.	8.	13.	2.
Average cell size (15)	0.06	0.058	0.052	0.043	0.057	0.04
Average number of cells (15)	16.53	16.95	19.02	23.2	17.45	24.46
Leaf *C*	34.	31.	15.	9.	14.	3.5
Average cell size (15)	0.063	0.057	0.04	0.042	0.045	0.041
Average number of cells (15)	15.76	17.45	24.63	23.27	22.02	24.16
Leaf *D*	33.	30.	18.	8.	12.	2.5
Average cell size (5)	0.094	0.068	0.054	0.046	0.042	0.045
Average number of cells (5)	10.6	15.48	18.18	21.33	23.49	22.17
Leaf *E*	33.	29.	16.	5.5	14.	3.
Average cell size (9)	0.067	0.074	0.036	0.035	0.047	0.033
Average number of cells (9)	14.83	13.37	27.42	28.07	21.27	29.98
Leaf *F*	30.	25.	20.	7.	20.	3.5
Average cell size (9)	0.085	0.062	0.046	0.045	0.051	0.046
Average number of cells (9)	11.68	15.91	21.37	21.8	19.29	21.47
Leaf *G*	50.	31.	22.	10.	15.	3.5
Average cell size (12)	0.06	0.079	0.042	0.038	0.04	0.033
Average number of cells (12)	16.49	12.56	23.45	25.77	25.54	29.64
Leaf *H*	37.	32.	15.	8.	16.	3.
Average cell size (11)	0.056	0.06	0.036	0.039	0.041	0.031
Average number of cells (11)	17.84	16.57	27.03	25.57	23.92	31.55
Leaf *I*	41.	31.	24.	7.	19.	3.5
Average cell size (9)	0.064	0.062	0.043	0.04	0.054	0.043
Average number of cells (9)	15.48	15.96	23.16	24.85	18.44	23.08
Average measurements of leaves	34.88	29.	18.88	7.94	14.25	3.
Average measurements of cells (100)	0.065	0.062	0.043	0.042	0.044	0.037
Average number of cells (100)	15.15	15.96	22.84	23.54	22.47	26.31
Ratio dimensions of leaf	1.2 : 1		2.37 : 1		4.75 : 1	
Ratio dimensions of cell	1.05 : 1		1.03 : 1		1.17 : 1	

cells by no means agrees with that of the corresponding dimensions of the leaves. While the difference between the length and the width of the linear leaves is almost four times greater than that of the basal leaves, the cells of the linear leaves are relatively only .11

longer than those of the round leaves. That is, the difference in these two leaf shapes is almost forty times as great as the difference in the shapes of the cells. Furthermore, the transitional leaves have proportionately wider cells than the basal leaves.

There is a considerable range of variability in the shape of the cells of any one type of leaf. For example, in a basal leaf, *D*, 33 mm. long by 30 mm. wide, the average length of the cells of the lower epidermis was 0.094 mm., the average width 0.068 mm., while in another leaf, *G*, 50 mm. by 31 mm., the average cell measurements were 0.06 mm. for the length and 0.079 mm. for the width. The great range of variability of the cell shape of each type of leaf may account for the slight difference between the ratios of the cell dimensions of the round, the narrow and the transitional leaves.

The decrease in cell size, that is, in both length and width, found in the linear leaves as compared with the basal leaves, is even more marked than in *Campanula rotundifolia*. The ratios between the corresponding dimensions of the cells of the three forms of leaves are given in TABLE V. It will be seen that the

TABLE V

LOBELIA ERINUS

Relative size of the cells of the lower epidermis of the three types of leaves.

	Length of cells	Width of cells
Transitional leaf : Basal leaf	.66 : 1	.67 : 1
Narrow leaf : Basal leaf	.67 : 1	.60 : 1

cells of the transitional and linear leaves, both of which grow on the stem and are produced at almost the same stage of development of the plants, have cells which are almost identical in size, although differing considerably from those of the earlier, radical leaves.

PLANTAGO MAJOR AND PLANTAGO LANCEOLATA

The leaves of the two species of plantain, *Plantago major* and *P. lanceolata*, differ greatly in shape. The largest and best developed leaves of each species that could be obtained, were chosen for comparison. *P. lanceolata*, when crowded, produces leaves which are somewhat dwarfed, particularly in their breadth, being

relatively only two-thirds to three-fourths as wide as is usual. Such leaves also were examined.

Measurements were made of the cells of the lower epidermis of such leaves of *P. lanceolata*, as well as those of the normal *P. lanceolata* and *P. major* leaves. Also the palisade cells of the two species of plantain leaves were compared. The results of these measurements are given in cell size and in cell number per millimeter in TABLE VI.

TABLE VI

PLANTAGO

Measurements of the length and the width of the leaves of two species of plantain, and of the corresponding dimensions of the cells of their lower epidermis and their palisade tissue in transverse section, expressed in millimeters and in number of cells to one millimeter. B = average size of cells in mm. C = average number of cells to 1 mm. Numerals in parentheses show the number of counts.

	Leaf		Cells of lower epidermis	
	Length	Width	Length	Width
P. major	176.09	110.06	*B*(100), 0.031	0.044
			C(100), 30.09	22.63
Ratio	1.6 : 1		.75 : 1	
P. lanceolata	310.3	32.63	*B*(100), 0.035	0.041
			C(100), 27.97	23.97
Ratio	9.2 : 1		.85 : 1	
P. lanceolata (narrow)	153.5	10.5	*B*(100), 0.032	0.038
			C(100), 30.71	25.81
Ratio	14.6 : 1		.83 : 1	

	Leaf		Palisade cells	
	Length	Width	Length	Width
P. major	48.	27.	*B*(30), 0.022	0.021
			C(30), 44.1	46.28
Ratio	1.71 : 1		1.04 : 1	
P. lanceolata	70.	23.	*B*(30), 0.021	0.021
			C(30), 46.92	46.79
Ratio	3.04 : 1		1 : 1	

In both species the palisade cells are quite round in transverse section. The cells of the lower epidermis of *P. major* are slightly shorter than those of *P. lanceolata*, but the disproportion does not approach that between the length and width of the leaves of the two species. The *P. lanceolata* cells are only 7 per cent. longer and 6 per cent. shorter than those of *P. major*.

I have plotted frequency curves for each species showing the number of times that a given ratio of the length to the width of the epidermal cells occurred. It would be difficult to determine,

from curves as irregular as these, the mean ratio of length to width in either species.

This does not mean that the shape of the lower epidermal cells is the same in both cases. While the difference does not lie in the length and width of the cells, their outlines are quite different, the cells of *P. major* being quite wavy in outline, while in both types of leaves of *P. lanceolata* the cells are only slightly wavy in outline. The cells of the normally developed and the narrow leaves of *Plantago lanceolata* are practically the same in shape and size.

LINUM ANGUSTIFOLIUM AND LINUM USITATISSIMUM

The leaves of *Linum usitatissimum* are lanceolate, those of *L. angustifolium* are oblong or oblong-elliptical. The leaves of both species are sessile, acute and entire. Those of *L. usitatissimum* are about as broad, but at least twice as long as the leaves of *L. angustifolium*. The cells of the lower epidermis and the palisade cells were measured in each species. The measurements show a striking similarity in the cell shape of these two species of *Linum*. The cells of *Linum usitatissimum* are only .04 longer than those of *L. angustifolium*, and show no relation therefore to the greater difference in their leaf dimensions.

CICHORIUM INTYBUS

The first leaves of the common type of *Cichorium Intybus* are entire but these are soon succeeded by other radical leaves which are distinctly lobed. The degree of lobing varies greatly in different plants, but the leaves of any one plant are quite similar in shape. For this reason all the leaves of *Cichorium Intybus* whose cell shape was measured were selected from one plant, which had deeply constricted leaves. The Witloof type of *Cichorium Intybus* is a cultivated variety of chicory, which has large and relatively entire leaves. All the leaves of this type studied were taken from the same plant. These, as well as the leaves of the common type of *Cichorium Intybus* with which they were compared, were basal leaves. In both, the cells of the lower epidermis near the midrib and near the margin of the broadest part of the leaf, and midway between these two regions were measured and their two dimensions compared with the length and breadth of the leaves to which they belonged (TABLE VII).

TABLE VII

CICHORIUM INTYBUS, COMMON TYPE

Maximum length and width of each leaf, the width of each leaf across the lobes, and the constricted portions, and the length and width of the cells of the lower epidermis in these two regions of the leaf. A = width of leaf from midrib to margin. B = average size of cells in mm. C = average number of cells to 1 millimeter. Numerals in parentheses show the number of counts.

Leaf Size			Constricted portion		Lobe below this constricted portion					
					Near Midrib		Midway out from midrib		Apex of lobe	
Length	Width		Length	Width	Length	Width	Length	Width	Length	Width
		A		2.		28.				
250	95	*B* (15)	0.36	0.29	0.03	0.028	0.33	0.03		
		C (15)	27.57	34.1	32.67	34.6	30.11	32.48		
		A		6.		28.				
220	61	*B* (15)	0.033	0.027	0.028	0.029	0.03	0.029		
		C (15)	29.48	36.8	35.65	34.28	32.99	33.8		
		A		6.		15.				
135	53	*B* (15)	0.025	0.029	0.026	0.027	0.034	0.023		
		C (15)	38.55	34.12	37.81	35.95	29.22	42.28		
		A		5.5		34.				
186	65	*B* (15)	0.037	0.027	0.03	0.03	0.032	0.027		
		C (15)	26.43	35.85	33.21	32.94	31.03	35.95		
		A		4.		29.				
229	71	*B* (15)	0.033	0.028	0.033	0.028	0.029	0.027	0.028	0.026
		C (15)	29.42	34.99	29.35	35.47	33.5	36.1	33.56	37.45
		A		4.		32.				
153	57	*B* (15)	0.033	0.029	0.029	0.028	0.034	0.028	0.027	0.029
		C (15)	30.	34.11	34.02	34.68	29.36	34.6	36.52	33.69
		A		4.		21.				
151	55	*B* (10)	0.034	0.025	0.03	0.032	0.026	0.026		
		C (10)	29.24	39.46	32.92	30.41	37.21	37.07		
		Av. *A*		4.5		26.				
Av. 189	Av. 65	Av. *B* (100)	0.033	0.028	0.029	0.029	0.031	0.027		
		Av. *C* (100)	30.14	35.92	33.7	34.23	31.62	35.99		
Ratio dimensions of cell.....			1.17 : 1		1.01 : 1		1.13 : 1			

The lower epidermal cells of the broadest lobes of each leaf were compared with those of the constriction immediately adjacent to it. The ratio of the average length to the average width of the cells is .04 greater in the constricted portion than in the middle region of the lobe, and .16 greater than in the lobe near the midrib. This rather slight difference is apparently due to the fact that the

cells in the constricted portions of the leaf are longer, rather than narrower, than the cells of the lobes, whereas in the leaf as a whole the difference is plainly one of greater breadth of the leaf in the lobed portion than in the constricted portion, the length

TABLE VIII

CICHORIUM INTYBUS, WITLOOF TYPE

Maximum length and width of the leaves of a cultivated chicory and corresponding dimensions of the cells of the lower epidermis in different regions of the leaf. A = width of leaf from midrib to margin. B = average size of cells in mm. C = average number of cells in 1 millimeter. Numerals in parentheses show the number of counts.

Leaf size			Basal portion		Broadest part of blade					
					Near midrib		Midway out from midrib		Marginal	
Length	Width		Length	Width	Length	Width	Length	Width	Length	Width
		A		6.		45.				
350	92	*B* (15)	0.062	0.029	0.032	0.032	0.038	0.026	0.027	0.024
		C (15)	16.01	33.98	30.35	30.87	26.15	37.18	35.82	40.5
		A		13.		52.				
386	105	*B* (15)	0.059	0.027	0.03	0.039	0.032	0.034		
		C (15)	20.04	36.59	32.43	25.5	30.98	29.34		
		A		13.		51.				
352	102	*B* (15)	0.055	0.03	0.033	0.033	0.034	0.033		
		C (15)	17.89	32.43	29.52	29.93	29.13	30.05		
		A		6.		48.				
412	104	*B* (15)	0.053	0.029	0.036	0.04	0.037	0.036	0.037	0.037
		C (15)	18.85	33.71	27.75	24.67	26.63	27.66	26.94	27.01
		A		8.5		50.				
472	94	*B* (15)	0.066	0.026	0.032	0.037	0.031	0.032		
		C (15)	14.95	37.17	30.65	26.42	31.29	30.69		
		A		8.		49.				
425	107	*B* (15)	0.062	0.03	0.041	0.034	0.033	0.033	0.029	0.026
		C (15)	15.92	32.42	24.06	28.58	30.04	29.43	33.5	37.68
		A		9.		51.				
350	104	*B* (10)	0.041	0.035	0.03	0.03	0.035	0.036	0.032	0.031
		C (10)	24.01	28.28	24.02	32.95	28.49	27.26	31.07	31.84
		Av. *A*		9.07		49.42				
Av. 404	Av. 99	Av. *C* (100)	0.055	0.029	0.034	0.035	0.034	0.032		
		Av. *B* (100)	17.95	33.76	28.62	28.19	28.98	30.38		
Ratio dimensions of cell.....			1.88 : 1		.98 : 1		1.04 : 1			

of the two regions being the same, or even less in the constricted portion. The cell shape in the wild chicory leaf is practically the same both in the lobes and the constrictions of the leaf.

The cells near the base of the Witloof chicory leaf are apparently modified in their shape by their relation with the numerous veins.

The lobing of the wild chicory leaf is not due to greater width of the cells in the lobes as compared with the constricted areas, but rather to the greater number of cells in the long axis of the lobe, which is almost at right angles to the midrib. This greater cell number is apparently due to a more rapid rate of division in the lobe cells as compared with those in the constricted regions (TABLE VIII).

The cells of the leaves of the Witloof variety are larger than those of the wild chicory leaves, but the shape of the cells is almost the same in both varieties. The ratio of the length to the width of the Witloof cells is 1.01 : 1, that of the wild chicory cells being 1.11 : 1.

SUMMARY AND CONCLUSIONS

Cell size

The cells of the plants above described show a considerable variability in size in the same tissue but that the average cell size for any one tissue of a species or variety, however, is a fairly constant and hereditary character, has been previously shown by Sanio, Amelung, Sachs, Strasburger and Conklin.

The cell size of closely related species, as *Linum usitatissimum* and *Linum angustifolium*, may be the same, which agrees with the conclusions of Amelung and Conklin, or again, in closely related varieties of the same species, as the common and Witloof types of *Cichorium Intybus*, the cell size may differ considerably, as was also proved to be true in certain plants investigated by Gates, Keeble, Neilson Jones, Jakushkine and Wawilow, and Sierp.

As Sanio, Jakushkine and Wawilow, and Sierp have already shown, the cell size in an organ depends in some degree on the stage of development of the plant at the time the organ was produced. Thus the transitional leaves of *Campanula rotundifolia* and *Lobelia Erinus* which are developed after the basal leaves, have smaller cells, while the linear leaves, which appear latest, have the smallest cells. In both these plants, the average cell size of each type of leaf is a constant characteristic. Differences in the size of any given organ of a species are due to differences in

the number of its cells, and not to variations in cell size. The extreme limits of the number of cells of which each type of leaf may be made up, are obviously determined by heredity, and the hereditary size of the organ is due to factors of periodicity in growth, which determine the rate and duration of cell division.

Cell shape

Livingston (1901) describes the cells of *Stigeoclonium* as having two characteristic shapes: a spherical form when growing in loose masses on the trunks of trees, in highly concentrated media, or when partially desiccated; and a cylindrical form, when growing in filaments in extremely dilute media. Instances like the above might lead one to believe that cell shape is largely a matter of environmental conditions, such as mutual pressure, turgor as influenced by environment, etc. However, there are unicellular algae, for example the desmids and diatoms, having a characteristic cell shape which cannot be due to pressure nor any simple turgor relations.

My studies show that the cells of the lower epidermis of the leaves of any species of plant, in the regions between the veins, have a characteristic length and breadth. The cell shape may, in other regions, be modified to a considerable extent by various factors, as by the presence of stomata, veins, etc. The relative length and breadth of the cells of any tissue may be the same in different species or varieties, as in *Linum usitatissimum* and *Linum angustifolium*, or it may be somewhat different, as in *Plantago major* and *Plantago lanceolata*.

Differences in the shapes of the leaves of the same plant, or of related species, are not correlated with corresponding differences in the shape of their cells. The linear leaves of *Campanula rotundifolia* and *Lobelia Erinus* are not composed of longer, narrower cells than those found in the round leaves, but have a larger number of cells in the long axis of the leaf. The cells of *Cichorium Intybus* are of the same size and shape in the lobed and in the constricted portions of the leaf.

The shape of the leaf obviously cannot be the result of the differences in cell shape but must rather be due to factors for periodically limiting the number and direction of the cell divisions in

each type of leaf. The form of incised leaves like those of *Cichorium Intybus* must be due to a factor or factors for differential periodicity, which determines that the rate or duration or both, of cell division, shall be greater in one part of the leaf than in another, thus producing the lobes and constrictions.

In concluding, I wish to express my gratitude to Dr. R. A. Harper, under whose direction these investigations were undertaken, for the many helpful suggestions he gave me throughout the course of this work. I also thank Dr. A. B. Stout, from whom I obtained my chicory material, for his kind interest and help.

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Two remarkable Discomycetes

EDWARD T. HARPER

(WITH PLATES 1–3)

1. UNDERWOODIA COLUMNARIS Peck

I have collected this rare plant in several localities in Michigan and Illinois. The first collection was on Neebish Island, Michigan, in August, 1897. A cluster of small plants about two inches high were found growing beside a path in balsam woods. The next year some larger plants were found growing among dead leaves in a ravine on Mackinac Island. In September three different collections were made on Neebish Island, and the photographs on PLATE 1 were taken. In May, 1908, the two plants shown on PLATE 2 were found on a hillside in open woods at Bureau, Illinois. A single plant was found at Neebish during the past summer.

The species was described and illustrated by Dr. Peck in the 43d Report of the New York State Museum, p. 78, *pl. 4* (1890), from plants found near Kirksville, New York, and sent to Dr. Peck by Professor Underwood. A note in Underwood's Moulds, Mildews and Mushrooms, p. 65 (1899), says that six plants were found in the same locality in three different years. Peck's description is accurate as far as it goes, but his account of the base and method of branching of the plant is incomplete. The plant is so unique in structure and so remarkable in habit and size that I have thought it worth while to discuss its structure and relationships on the basis of my specimens.

Peck's illustration shows the part above the ground only, and he describes it as stemless and everywhere acigerous. This led Schroeter to place the genus among the Rhizinaceae. The plant does, however, have a short stem and is more or less bulbous at the base. The lower margin of the hymenium is uneven, running down in points on the stem while naked strips extend upward for short distances into the hymenium as in some species of *Geoglossum*. There is a definite though inconspicuous margin to the

hymenium and in dried plants the hymenium becomes reddish brown where the asci are numerous, while the stem remains whitish. The base of the plant is rounded like the base of species of *Morchella*. No thick mycelial root or sclerotium of any kind was found.

Sometimes the clubs are simple as shown on PLATE 2 and in Peck's illustration but they usually divide into fingers. The plant on PLATE 1 was divided near the middle. The halves have split and sprung apart as shown in *B*. The left branch shown at *A* is forked near the apex. The right branch was nearly destroyed by insects but appeared to have been more deeply divided. Other plants in the collections were divided a little below the middle. PLATE 2 shows two plants, one of which has been sectioned, closely caespitose and apparently connected at the base. In the cluster of small plants first discovered there were at least three connected at the base.

The whole interior of the plant—bulbous base, stem and ascoma—is perforated by irregular longitudinal cavities, as shown in the section on PLATE 2, *A*. The walls of the cavities are of nearly uniform thickness. The interior of the walls is composed of a mesh of septate hyphae 6–8μ in diameter. The cavities are lined with a palisade layer of regular, septate hyphae about 6μ in diameter. The layer is about 50μ thick and there are three or four septa in each hypha. The appearance of a cross section of one of the walls is like that shown in Hesse's Hypogaeen Deutschlands, *pl. 18, f. 12* (1894), except that the interior is composed entirely of septate hyphae.

The outside walls are covered with the hymenium on the outside and the palisade layer on the inside. The surface of the hymenium is wrinkled and corrugated, PLATE 2, *C*, but there appears to be no definite relation in position between the wrinkles of the hymenium and the internal cavities. The interior of the walls is composed of hyphae, and there appears to be no definite subhymenial layer. A palisade layer like that on the walls of the interior cavities covers the stem and base of the plant.

The asci, PLATE 2, *B*, are club-shaped, 10–12 × 160–200μ. They open by a lid as far as I can make out but I have not been able to find empty asci, which Boudier says must be examined to deter-

mine the nature of the opening. The character of the plant and the spores is that of Boudier's division Opercules. The paraphyses are septate, a little longer than the asci, slightly thickening upward and somewhat curved at the apex, 4–6μ in diameter.

The colors of the plant are whitish or cream colored outside and pure white within.

I have rewritten Peck's description to include the form of the base and method of branching, as follows:

Ascocarps single or caespitose, simple or more or less deeply and somewhat dichotomously divided, divisions columnar, straight or slightly curved, sulcate-costate and uneven; ascigerous layer definite but not separated from the short stem. Base even or slightly bulbous, interior perforated by irregular longitudinal cavities, separated by thin walls, whitish or brownish outside, pure white within, cavities lined with a regular palisade layer of septate hyphae; asci club-shaped, 10–12 × 160–200μ; paraphyses slightly longer than the asci, rarely branched, septate, 4–6μ in diameter; spores tuberculate, hyaline or slightly colored, elliptical, 10–13 × 18–24μ.

Varying greatly in size, 5–35 cm. high, 2–5 cm. thick.

Growing on the ground among grass or dead leaves in mixed woods.

Underwoodia columnaris is not closely related to any known discomycete. It forms a monotypic genus, as the term is usually understood. It appears to be the only representative of its group.

The group arrangement is especially applicable to the large discomycetes, for the groups are few and well marked; and, while the forms within them are closely related, the kinship of the groups themselves appears remote. Apart from *Underwoodia* there are only seven groups in the family Helvellaceae in our region: the *Morchella esculenta*, *Morchella hybrida* and *Verpa digitaliformis* groups in the *Morchella-Verpa* series and the *Gyromitra esculenta*, *Gyromitra infula*, *Helvella crispa* and *Helvella elastica* groups in the *Gyromitra-Helvella* series. In the Geoglossaceae there may be about thirteen groups, nine of which are in the large *Geoglossum* series and one each in *Spathularia*, *Cudonia*, *Leotia* and *Vibrissea*. The groups are also few and well defined among the larger Pezizaceae. The order Helvellales is based on little more natural relationship than that its members are the large conspicuously stemmed discomycetes.

Forms within the groups offer a most fruitful field for ecological and comparative study. Most of the groups of large discomycetes, such as the *Verpa*, *Cudonia*, *Leotia*, and *Geoglossum glutinosum* groups, appear in a variety of forms. In some groups the forms are very abundant and variable. Boudier has named and given beautiful illustrations of twenty-three forms in the *Morchella esculenta* group, offering a fine opportunity for students to compare other *Morchella esculenta* floras with that of France. Durand lists seven forms in the *Geoglossum glabrum* group. *Underwoodia* is so rare that its variation is little known, though it may have had a bloom period at some time in the past.

But while the kinship and variation of *Underwoodia* are unknown it possesses a striking combination of characters found singly in other groups. Most of these characters are more highly developed than in other groups where they occur and this gives to *Underwoodia* a unique position and a special interest. I can only briefly compare the most striking characters and do it without implying any close kinship between *Underwoodia* and the groups in which similar characters are found.

The cancellated stem of *Underwoodia* is more highly developed than in any other discomycete. It contrasts strongly with the hollow stems of species of *Morchella* and the solid stems of the Geoglossaceae. The character is found in the *Acetabula vulgaris* and the *Helvella crispa* groups, but the stems in these groups are deeply sulcate as well as cancellate, the cavities are much less regular and the walls of the cavities as far as I have examined them are not covered with a regular palisade layer. The stems of species of *Morchella* often have a few cavities near the base. They are very markedly developed in the specimen of *Gyromitra gigas* illustrated by Boudier (Icon. Mycol. *pl. 221*. 1904). Such cavities are not lined with a palisade layer of hyphae.

Many discomycetes have lacunae and cavities in the stem. An interesting case for comparison with *Underwoodia* was identified for me by Durand as *Lachnea* (or *Macropodia*) *semitosta*. The stem bears a close resemblance to that of *Underwoodia*. There are a few sulcations on the outside, but the walls of the cavities are not lined with such a regular palisade layer. *Macropodia semitosta* is remarkable in the development of the cancellated stem. Note the

illustration of *Peziza semitosta* in Cooke's Mycographia, *f. 109* (1879). The palisade layer lining the cavities in the body of the fungus is most highly developed in species of Hypogaei, but in them it is connected with the hymenium. Bucholtz derives the Helvellaceae from *Lachnea* through the Hypogaei.

The cancellated stem is combined in *Underwoodia* with a club-shaped ascoma, not cup-shaped or saddle-shaped as in the *Acetabula* and *Helvella* groups. Such club-shaped ascomata are found in the groups of the *Geoglossum* series. In size, however, in substance, in the spores, and probably in the opening of the asci *Underwoodia* is widely removed from any of the groups in that series. The hymenium is also more sulcate than in species of *Geoglossum* and resembles in this respect the hymenium of *Verpa*. Compare Boudier's illustrations on *pl. 219* and *220*. We may also compare the ascoma of *Gyromitra gigas* referred to above. *Gyromitra gigas*, as illustrated by Boudier in *pl. 221*, is nearer in general shape and appearance to *Underwoodia* than any other discomycete with which I am familiar.

The spores of *Underwoodia* have a tuberculate wall and in this respect are more highly developed than is usual among the Helvellaceae, the other species of which have smooth, hyaline spores.

The question whether *Underwoodia* is a gymnocarp or an angiocarp cannot be settled without the young stages. In the ascoma of the species of *Helvella* the young hymenium is overgrown by surrounding tissue as in very many cup fungi and the same is true of the elements of the compound hymenium of *Morchella*. The hymenium of *Underwoodia* does not appear to have been so overgrown at any time, but whether it was covered at any stage with a weft of fibers, as is the case with many of the Geoglossaceae is not known. Nor is it known whether the hymenium originated on or below the surface of the primitive ascocarp. Questions as to the protection of the young hymenium in the discomycetes are not yet settled.

The high development of the different characters in *Underwoodia* gives it a most important position. It is one of the largest and certainly the most highly developed of all the discomycetes.

2. PUSTULARIA GIGANTEA Rehm

In July, 1899, I found some large cup fungi on the ground among dead leaves on Mackinac Island, Michigan. Later I sent them to Dr. H. Rehm, who described them as a new species under the name *Pustularia gigantea*. The description was published in Annales Mycologici (3: 517. 1915). I have since found the plant several times in coniferous woods on Neebish Island. In September, 1907, it was abundant in a piece of cedar and balsam woods, and I secured the photograph of the opened plant, PLATE 3, A, and preserved a number of unopened plants in alcohol, from which the photograph of the section, B, was made. The specimens sent to Dr. Rehm were dried and somewhat torn, so that they did not show the peculiar folding in of the edges of the apothecium and the way in which the mature plants burst open, which are two of the most striking characters of the species.

The unopened apothecia are irregularly ellipsoid with a deep groove across the top. The apothecia often occur in clusters in which the orientation of the members is irregular. The surface of the apothecia is nearly smooth, whitish in color, and much soiled by the earth or mould in which the plants are buried.

The apothecia have a definite interior structure which is shown in PLATE 3, B. This figure represents a vertical section cut from the center of an unopened apothecium. There is no stem and the flat under surface lies directly on the soil, with which it is connected by strands of white mycelium. Quite frequently the connection with the substratum is lost, as is the case with the Hypogaei.

The cup is roughly and partially divided into two chambers by the infolding of the edges of the apothecium. The chambers can be recognized in all the plants examined, though they are at times more or less distorted. The infolded edges extend to the bottom of the cup. In a section like this made through the center of the apothecium the infolded walls are divided at the base. In sections near the ends of the apothecium they are united. The walls have been infolded till the usual apical opening or mouth of the cup in other Pezizaceae lies on the bottom of the cup. Neither the lips nor the walls are grown together, though they are pressed closely against each other. In the section before us the walls have sprung apart. The lips are like those of other cup fungi with the hypo-

thecium extending a little beyond and embracing the hymenium. The bottom of the cup is thickened and raised into a sort of cushion covered like the rest of the interior by the hymenium. Such a cushion is evident on the bottom of all the cups examined. Around the cushion is a narrow zone which is destitute of hymenium. It has apparently resulted from a rupture of the hymenium during growth. In the larger chamber is an irregular outgrowth covered by the hymenium such as may occur in almost any position on the hymenium of these plants.

An end section of another specimen shows an apothecium in which the basal cushion is very large. The chambers are irregular and there are several minor cavities. The general structure is however the same as in the plant figured on PLATE 3. The basal cushion in this second specimen is hollow and it was deeply indented on the under side in a zone around the central portion, which was attached to the soil as a sort of stem.

When the apothecia are mature and the growth tension becomes great; instead of opening at the mouth as in most species of *Peziza*, the walls of the chambers burst irregularly as shown in PLATE 3, *A*. The appearance of such opened plants is striking. The walls of the internal cavities are pure bluish white and the thick reflexed segments give the plant the appearance of a large white flower. When the weather is unfavorable to rapid growth the apothecia do not open as far as my observation goes but dry up or decay without exposing the hymenium. Sometimes irregular openings are found in the walls of old plants.

In regular plants the walls of the apothecia are of nearly equal thickness throughout. They are covered on the inside by the hymenium. The hypothecium is made up of irregular septate hyphae of different diameters with many large irregular cells and cavities, especially in the center. The hyphae are much more dense directly beneath the hymenium where they form an indefinite subhymenial layer. On the outside there is a compact cortical layer of hyphae which run somewhat parallel to the surface. In the center of the walls the tissue is looser and the cells larger. Often the tissue breaks down and leaves hollow spaces in the walls. as can be seen in the sections.

The asci are long and narrow and closely packed together with

relatively few paraphyses. They measure 10–12 × 200–300μ. They are linear for most of their length, rounded-truncate at the apex and narrowed near the base. The base is enlarged and irregular. The paraphyses are about 2μ in diameter, slightly enlarged at the upper end, rarely branched and with few septa. The spores are oblong with rounded ends, smooth, usually with two oil drops when mature, 5–8 × 10–14μ.

Rehm placed the plant in the genus *Pustularia* and compared it with *Pustularia vesiculosa*, noting that it differed from that species in the larger size and smaller spores. According to Rehm's key *Pustularia* contains species of fleshy Pezizaceae, which have smooth and entire cups, asci turning blue with iodine, elliptical spores and sessile apothecia. It includes species like *Peziza vesiculosa*, *P. Stevensoniana*, and *P. coronaria*. Boudier disregards the surface of the apothecia and places species like *Peziza coronaria* and *Sepultaria sepulta* in a genus *Sarcosphaera*, on the ground that they are semi-subterranean with the apothecia closed at first and bursting irregularly at maturity. *Pustularia gigantea* is semi-subterranean in its habit and bursts irregularly at maturity and might be placed in this genus, but it has a definite mouth the walls of which have simply become infolded during growth.

The natural arrangement of the species of Pezizaceae has not yet been discovered. All that was said about the groups of the Helvellaceae above applies equally to the groups of the large cup fungi. As Dodge has emphasized, a knowledge of the early stages is a necessary prerequisite of a natural classification.

It is not certain to which group *Pustularia gigantea* belongs. It is not close to *Pustularia vesiculosa*, as Rehm suggests, for in addition to the difference in the size of the spores the subterranean habit and character of the mouth are very different from that species. Our collections of *Pustularia vesiculosa* have mouths of the ordinary form and grow in the mulching about trees and on manure heaps. They agree with Lloyd's photograph in Hard's Mushroom, *f. 432* (1908). *Pustularia gigantea* appears to be closer to *Peziza coronaria*, for that species is subterranean. Boudier's illustration, *pl. 302*, resembles our expanded plant. Cooke's illustration in Mycographia, *f. 238*, agrees in size and method of opening, and the same is true of Kalchbrenner's illustration of *Peziza coro-*

naria var. *macrocalyx* (Icon. Select. *pl. 40, f. 2*). The spores also are nearer in size to those of *Peziza coronaria* than to those of *P. vesiculosa*. Saccardo's Sylloge (**8**: 81. 1889) gives the spores of *P. coronaria* 8–9 × 15–18*μ*. The spores of *Pustularia gigantea* are often 8 × 14*μ*, though Rehm gives 5–6 × 10–12*μ*. The descriptions of *Peziza coronaria* do not, however, give the internal structure of the unopened apothecia. It is supposed that the young plants have no evident mouths. The species of *Sepultaria* also are said to be closed at first and to open irregularly. Yet what is known of the structure of the cup fungi suggests that in all these forms the hymenium has been overgrown by surrounding tissue, and the location of the mouth should be determinable even in young unopened apothecia. *Pustularia gigantea* is very enlightening on this point and the unopened apothecia of species like *Peziza coronaria* should be carefully examined to see if there is not evidence of the location of the mouth. It is uncertain whether *Pustularia gigantea* should be associated with *Peziza coronaria* or placed in a group by itself. Further observation may bring to light other more closely related forms.

The most striking feature of *Pustularia gigantea* is the degree in which the walls of the apothecia are infolded. It is very common among the discomycetes for the hymenium to be covered by the surrounding tissue during the formative period. In small species of *Peziza* the ascoma usually remains circular, but in large plants the walls of the cup are flattened and folded together from the sides. This is also true of species of *Helvella* which have a cup-shaped or saddle-shaped ascoma. The saddle-shaped ascoma in the *Helvella elastica* group is folded and flattened in the same way when young and later opens at the ends instead of in the middle giving it the characteristic saddle-shaped form.

Bucholtz has shown that in many of the Tuberaceae the hymenium is formed on the outside of the ascocarp and then overgrown by surrounding tissue until it is entirely enclosed in cavities of the fruit body. *Pustularia gigantea* has many characters in common with the Tuberaceae. The closed chambers, subterranean habit and loose connection with the soil are all suggestive of the Tuberaceae. We need only mention the Hysteriaceae to show how common the inrolling of the disk and consequent covering of the hymenium is among the discomycetes and their allies. The

striking feature of *Pustularia gigantea* is the extent to which the walls are infolded The mouth is completely inverted and lies on the bottom of the cup. In this the plant appears to be unique.

Explanation of plates 1–3

PLATE 1. UNDERWOODIA COLUMNARIS Peck

A, upper half of the left branch of a large plant; *B*, lower half of the plant.

PLATE 2. UNDERWOODIA COLUMNARIS Peck

A, longitudinal and cross sections; *B*, ascus and paraphyses; *C*, one of a pair of plants grown together at the base.

PLATE 3. PUSTULARIA GIGANTEA Rehm

A, expanded plant. *B*, vertical section through an unopened apothecium; *C*, asci and paraphyses.

INDEX TO AMERICAN BOTANICAL LITERATURE

1916-1917

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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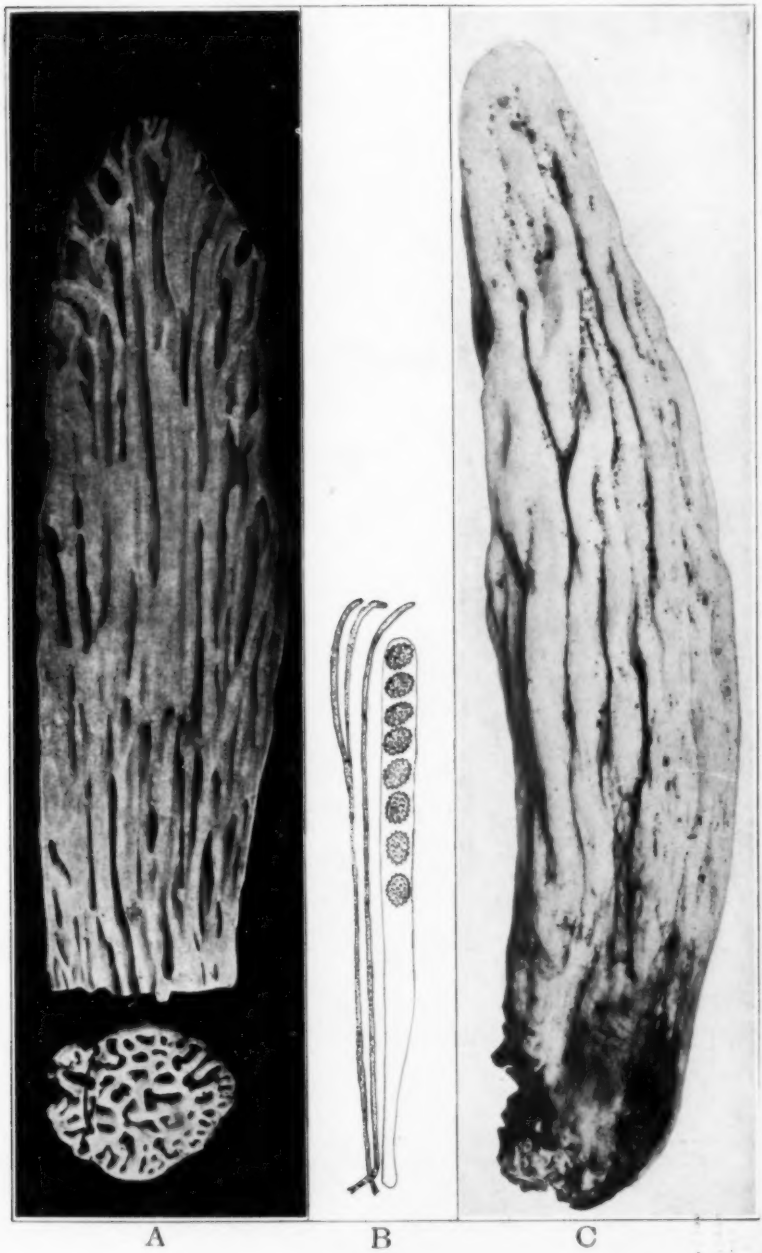
UNDERWOODIA COLUMNARIS PECK



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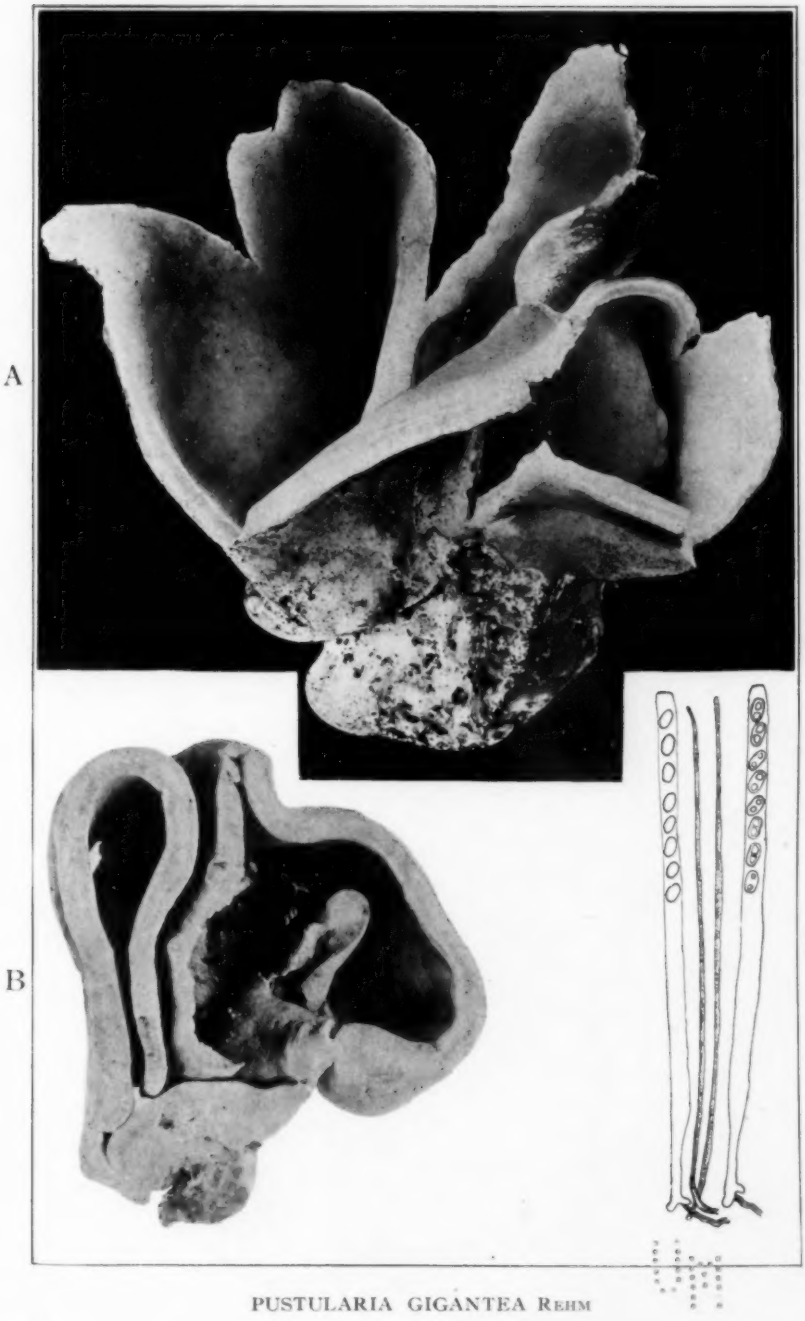

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